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# The big bad pig: niche conservatism and the invasive potential of the wild boar

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## Summary

1. Niche conservatism, i.e. the retention of a species fundamental niche through evolutionary time, is a cornerstone for biological invasion assessments. The fact that species tend to maintain their original climate niche allows predictive maps of invasion risk to anticipate potential invadable areas. Unraveling the mechanisms driving niche shifts can shed substantial light on the management of invasive species.
2. Here, we assessed niche shifts in one of the world's worst invasive species: the wild boar *Sus scrofa*. We also predicted potential invadable areas based on an ensemble of three ecological niche modeling methods, and evaluated the performance of models calibrated with native *vs* pooled (native plus invaded) species records. By disentangling the drivers of change on the exotic wild boar population's niches, we found strong evidence for niche conservatism during biological invasion.
3. Ecological niche models calibrated with native *vs* pooled range calibration scenario predicted convergent areas. Also, observed niche shifts are mostly explained by niche unfilling, i.e. there are unoccupied areas in the exotic range where climate is analogous to the native range.
4. Niche unfilling is expected as a result of recent colonization and ongoing dispersal, and was potentially stronger for the Neotropics, where a recent wave of introductions for pig-farming and game-hunting has led to high wild boar population growth rates. The invasive potential of wild boar in the Neotropics is probably higher than in other regions, which has profound management implications if we are to prevent their invasion into species-rich areas, such as Amazonia, coupled with expansion of African swine fever and possibly great economic losses.
5. Although the originally Eurasian-wide distribution suggests a pre-adaptation to a wide array of climates, the wild boar worldwide invasion does not exhibit evidence of niche evolution. The invasive potential of the wild boar probably lies on the reproductive, dietary and morphological characteristics of this species, coupled with behavioral thermoregulation.



**Key-words** Biological invasion; conservation biogeography; feral pig; invasive alien species; ecological niche models.

## Introduction

Assessing invasion risk and managing invasive species is a worldwide conservation, economic and social issue (Strubbe, Beauchard & Matthysen 2015) and niche shifts during biological invasions are one of the hot topics of current scientific debate (Guisan *et al.* 2014). In fact, understanding processes that drive changes in species fundamental niches is important for ecology and evolution (Wiens & Graham 2005; Pyron *et al.* 2015), and pivotal for understanding biological invasions (Broennimann *et al.* 2007; Guisan *et al.* 2014). A species "fundamental niche" can be defined as the set of environmental conditions where a species can persist indefinitely (Hutchinson 1957). Competition and other negative interactions lead to reductions in the fundamental niche to create the "realized niche" (Hutchinson 1957), or the "biotically reduced niche" (Peterson *et al.* 2011). In this sense, the "invadable niche" would be the portions of the fundamental niche, non-restricted by biotic interactions, but unreachable due to geographic dispersal limitations (Peterson *et al.* 2011).

Potentially invadable areas have historically been assessed through the study or models of ecological niche, which are based on the assumption that climatic similarity between native and exotic ranges is an *a priori* condition for the establishment of an alien species (Peterson 2003; Thuiller *et al.* 2005; Jiménez-Valverde *et al.* 2011). This assumption is possible because species fundamental niches are not likely to change over short-to-moderate time spans (Peterson 2011). Given that these niches exhibit little or no climatic niche differentiation, this process of niche conservatism is expected during biological invasion (Peterson 2003, 2011). Therefore, by determining climate tolerances from species native geographic range, climatically matching regions in non-native ranges can be assessed and

mapped (Thuiller *et al.* 2005; Jiménez-Valverde *et al.* 2011). If climatic conditions therefore pose long-term and stable constraints on species geographic distribution, potentially invadable areas can be anticipated with relative confidence (Peterson 2003).

Although exciting in their potential for guiding management decisions, ecological niche models can only accurately predict potentially invadable areas when niche conservatism is supported. However, initial studies on niche conservatism revealed contrasting patterns of niche shift due to tests of different null hypotheses (Peterson 1999; Graham *et al.* 2004). After Warren *et al.* (2008), niche conservatism was thought to be best measured in terms of statistical difference, i.e. "niche similarity" and "niche equivalence". Despite their transparency, the similarity and equivalence tests only reveal statistically significant differences on species climatic niches, but not the causes underlying niche shifts (Petitpierre *et al.* 2012; Strubbe *et al.* 2013; Guisan *et al.* 2014). Hence, absolute values of "equivalency" and "similarity" have little biological meaning unless niche shifts are disentangled into their main drivers of change, namely "niche unfilling" and "niche expansion" (Petitpierre et al., 2012; Guisan et al., 2014). In addition to detect of niche shifts, decomposing niche changes in terms of niche expansion and unfilling can shed substantial light on the ecological processes driving biological invasions (Broennimann et al., 2012; Guisan et al., 2014).

Currently present in all continents, except in Antarctica, the wild boar is a member of the family Suidae from Eurasia and North Africa. The wild boar is the oldest intentionally introduced mammal species (for bush meat) and is now one of the most widely distributed

species in the world (Long 2003). Biological traits of the species partially explain its invasive success. Wild boars have fast population growth rates (Taylor *et al.* 1998) and feed opportunistically on many plants and animals (Ballari & Barrios-García 2014). Population top-down control by predators is limited throughout its native and exotic ranges due to worldwide small density of large carnivores (Estes *et al.* 2011; Barrios-Garcia & Ballari 2012) and widespread defaunation of natural areas (Dirzo *et al.* 2014). Wild boars also possess weaponry and a low centre of gravity that prevents their preferential capture by all but the largest felids (Hayward, Jędrzejewski & Jêdrzejewska 2012). Further, their extensive native distribution across Eurasia and North Africa suggests a pre-adaptation to wide array of climatic conditions (Long 2003; Barrios-Garcia & Ballari 2012). In this paper, we assessed the invasive potential of the wild boar *Sus scrofa* globally. Our aim was to test whether wild boars and their hybrids have substantially changed their climatic niches during their global invasion. In addition, we mapped potentially invadable areas, where allowed by niche conservatism assumptions.

## Materials and methods

### THE WILD BOAR

Wild boars (*Sus scrofa*) are ecosystem engineers that turn extensive areas of leaf litter, soil and vegetation, and may ultimately affect fire regimes (Hayward *et al.* 2016). While the impact of that rooting behavior on biodiversity is controversial (Siemann *et al.* 2009), the same is not true for economic losses. Wild boar rooting damages crops and husbandry, causing economic losses up to 800 million dollars a year in the USA alone (Pimentel, Zuniga

120 & Morrison 2005). Wild boars damage various vegetable crops (Pimentel *et al.* 2005; Herrero
121 *et al.* 2006; Ballari & Barrios-García 2014) and also transmit and are reservoirs for several
122 diseases to humans and livestock (Barasona *et al.* 2014). Impacts of wild boars on wildlife
123 span predation (Ballari & Barrios-García 2014) to habitat and nest destruction (Barrios-
124 Garcia & Ballari 2012). Competitive interaction with wild boar leads to native species
125 exclusion, especially peccaries (Gabor & Hellgren 2000) and other species of the genus *Sus*
126 (Frantz *et al.* 2016). Despite those negative effects, in some particular areas – such as the
127 Brazilian Pantanal – wild boars are supposed to be a preferential target for bush meat hunters
128 and may thus release native peccaries from over-harvesting (Desbiez *et al.* 2011), although
129 this lacks empirical validation.

130

131 As they are primarily raised for meat, domesticated pig breeds were selected to increase traits,
132 such as fecundity and population growth rate. Escaped domestic pigs hybridize with wild
133 populations and transmit to them those artificially selected traits, which enhances hybrid
134 fitness (Fulgione *et al.* 2016). Hybrid pigs have therefore inherited higher fertility rates and
135 larger litter size from their domestic relatives (Fulgione *et al.* 2016), while retaining
136 sociability, coupled with associated large group herds, and flexible climatic tolerance from
137 their wild ancestors (Marshall *et al.* 2014). The impact of hybrid pigs on both biodiversity
138 and the economy can therefore be even harder than that of wild populations, although those
139 effects are still to be addressed in the scientific literature (Barrios-Garcia & Ballari 2012).

## DATA COLLECTION

We collected occurrence data for the wild boar and its hybrids [henceforth jointly named "wild boars"] from different virtual databases, namely the Global Biodiversity Information Facility (GBIF; www.gbif.org), the VertNet (www.vertnet.org), the Biodiversity Information Serving Our Nation (BISON; www.bison.usgs.ornl.gov), the Berkeley Ecoinformatics Engine (Ecoengine; www.ecoengine.berkeley.edu), the iNaturalist (www.inaturalist.org) and the Invasive Species Compendium (ICS; www.cabi.org). In addition, we exhaustively searched non-formal sources of wild boar occurrence information, primarily game hunting or wildlife sightseeing websites, such as the "Rede Aqui Tem Javali" in Brazil (aquitemjavali.blogspot.com.br), the "Wild Boars in Canada" (wildboarcanada.ca), and "Feral Scan" in Australia (www.feralscan.org.au). A strong geographical bias towards European countries was found in the distribution of wild boar occurrence records within native distribution. Thus, to improve characterization of the niche space, we did a literature survey on wild boar occurrences from less sampled regions within the native distribution (see Table S1). All occurrences from virtual databases were downloaded with the function *occ* from R package (R Development Core Team 2016) *spocc* (Scott *et al.* 2016), and occurrences from other sources were downloaded manually.

Native distribution was defined based on the IUCN range map for *Sus scrofa* (Oliver & Leus 2008), obtained at www.iucnredlist.org. The use of IUCN range maps to identify species native distribution is considered useful for large-scale modeling studies, as well as to conservation planning, management and wildlife monitoring (Rodrigues *et al.* 2006). We also included occurrences up to 200 km from the existing border of the species native range map.

Occurrences farther than that to the native polygon were removed from the "native dataset". By doing so, we accounted for possible uncertainties on the borders of IUCN range maps, to consider highly updated – though perhaps imprecise – species records. A total of 2283 occurrence records was then collected, from which 688 belonged to native distribution, 168 of them to the Australian region, 609 to the Nearctic region, and 736 to the Neotropical region (Fig. 1, Appendix S1). Those records cover years 1970 to 2016. Spatial autocorrelation was minimized by randomly removing occurrences less than 0.5 degree of latitude/longitude from each other, from the whole dataset (both native and exotic ranges). This procedure has minimized problems related to spatial autocorrelation in other niche shift studies at the biogeographical scale (Broennimann *et al.* 2012; Strubbe *et al.* 2015).

Climate data was produced from interpolation of ground weather stations, from year 1950 to 2000, downloaded from the WorldClim website (www.worldclim.org/version1) and downscaled to 0.5 degrees of latitude/longitude. All WorldClim bioclimatic predictors were used for tests of niche equivalence/similarity between native and exotic ranges, but only five were used to predict potentially invadable areas for the wild boar. A factor analysis with Varimax rotation was used to select uncorrelated variables and to avoid collinearity issues (Table S2). Five non-correlated variables were used to fit ecological niche models: BIO2: Mean Diurnal Range (Mean of monthly (max temp - min temp)); BIO5: Max Temperature of Warmest Month; BIO14: Precipitation of Driest Month; BIO15: Precipitation Seasonality (Coefficient of Variation); BIO16: Precipitation of Wettest Quarter.

## NICHE EQUIVALENCE/SIMILARITY TESTS

We used all predictors at first because tests of niche equivalence/similarity are best performed with the PCA-env method (Broennimann *et al.* 2012). The PCA-env is calibrated with the full background, i.e. environmental conditions of both native and exotic range, and reduces environmental data dimensionality to the first two main axes of the principal component analysis (PCA). That full background is then compared to the areas effectively occupied by species on each of its ranges. Niche overlap between native and exotic range is measured in terms of Schoener's *D*, which ranges from no overlap, 0, to complete overlap, 1 (Schoener 1974; Warren *et al.* 2008).

The observed niche overlap is then compared to random measures of niche overlap. Niche equivalence and similarity tests are based on comparisons of observed measures of niche overlap to random overlap values, although different null hypotheses are thereby tested. Niche equivalence tests, as initially proposed by Graham et al. (2004), ask whether the compared niches are indistinguishable from each other. Rejection of the null hypothesis on niche equivalency tests indicates that native and exotic niches are not identical (Broennimann *et al.* 2012; Strubbe *et al.* 2015). Niche similarity tests, on other hand, were first used in Peterson et al.'s (1999) work, and test whether niche models calibrated for one species (or population, in our case) predict other species occurrences better than expected by chance. The niche similarity null hypothesis is that of retained niche resemblance and its rejection indicates that niches are more different than expected by chance. Null hypotheses tests were repeated 1000 times for each biogeographical region and *p*-values were computed at a 5% level of confidence.

Following Broennimann et al. (2012), niche changes between native and exotic populations were directly measured in a gridded environmental space, not in the geographic space. Kernel density functions were used to produce smoothed densities of both occurrences and environmental availability. Explicitly incorporating environmental availability into niche shift measures reduces erroneous detections of niche changes due to uneven distribution of climate conditions on native and exotic ranges (Guisan *et al.* 2014). Niche shift analyses were done using the *ecospat* R package (Randin *et al.* 2016).

Niche equivalence and similarity tests only verify whether niche shifts have occurred, but do not address their causal mechanisms. To understand the wild boar invasion process, we disentangled niche changes into the processes of unfilling and expansion. Niche unfilling is observed when some environmental conditions within the native niche are available, but unoccupied in the exotic climate (Guisan *et al.* 2014). Those unoccupied areas probably result from recent colonization and ongoing dispersal. In niche unfilling, the exotic niche is a subset of the native niche, and the species will eventually occupy all available niche space within exotic range, unless biological interactions restrict range expansion (Guisan *et al.* 2014). Niche expansion, on the other hand, is the result of occupancy of non-analogous climatic conditions to the native range. In other words, niche expansion is observed when the species occupies climate conditions to which it is not supposedly adapted, based on its native distribution climatic limits. Such occupancy in non-analogous climates is probably due to ecological or evolutionary changes on its fundamental niche (Guisan *et al.* 2014).

Observed niche expansion can also be the outcome of the constrained nature of a species realized niche. Across an accessible geographic distribution, a species may not occupy its full fundamental niche due to extant or past biotic interactions (Soberón & Peterson 2005; Soberón 2007; Peterson *et al.* 2011). Also, there may be environmental conditions that are favorable to a species persistence, but non-existent throughout the species geographic range (Barve *et al.* 2011). All those conditions may limit the observed occupancy of certain environmental conditions that do belong to the fundamental niche (Hutchinson 1957). Therefore, observed niche expansion can also result from occupancy of regions within a species fundamental niche, but outside its geographically accessible area and/or restricted by negative biotic interactions. Also, the correlative nature of the techniques used to disentangle niche shifts into unfilling and expansion implies that a species niche will be always calibrated using observed occurrences from the realized niche (Guisan *et al.* 2014). Assessing the whole fundamental niche and knowing for sure all the exact conditions favorable for a species is nearly impossible. Therefore, asserting niche expansions may be a doubtful task.

Predicting potentially invadable areas for invasive species is only possible when: 1) changes in a species climatic niche are not observed or 2) observed niche differences are not caused by evolutionary changes in the species fundamental niche (Jiménez-Valverde *et al.* 2011; Strubbe *et al.* 2013, 2015). If the exotic niche is a subset of the native one, and niche shifts are therefore caused by niche unfilling rather than expansion, then an ecological niche model calibrated with climatic conditions where the species is known to occur may accurately predict invasion potential (Peterson 2011; Jiménez-Valverde *et al.* 2011; Strubbe *et al.* 2015).

253 Otherwise, the essential assumption of equilibrium between the species distribution and
254 climate tolerances is violated (Early & Sax 2014). In cases where climatic equilibrium is not
255 supported, forecasts of invasion risk based on correlative models may not be reliable (Early
256 & Sax 2014).

257

258 ECOLOGICAL NICHE MODELS

259 For cases exhibiting evidence for niche conservatism or niche unfilling as the main driver of
260 niche changes, we predicted potentially invadable areas for the wild boar using ecological
261 niche models. Ecological niche models are correlation procedures that capture environmental
262 conditions within which the species is known to be present, based on occurrence and
263 environmental data from geographic information systems (Broennimann & Guisan 2008;
264 Jiménez-Valverde *et al.* 2011). Original invasion risk assessments attempted to predict
265 potentially invadable areas from climatic conditions present in the species native range
266 (Peterson 2003; Thuiller *et al.* 2005). The idea behind this approach is that evolutionary
267 changes on species fundamental niches are not likely to occur within the timescale of
268 anthropogenic species invasions (Peterson 1999, 2011). Therefore, if climatic constraints
269 create evolutionary markers carried away during species transportations, then species are
270 supposed to preferentially occupy areas climatically similar to those where they evolved
271 (Peterson 2011).

272

273 Although the predictive accuracy of ecological niche models can often be high, the native-
274 based approach does not incorporate possible niche shifts that may occur during biological

invasions (Tingley *et al.* 2014). To allow for less restrictive models in terms of niche conservatism, the use of all occurrences from locations where a species is known to occur has been suggested as a step forward on invasion risk assessments (Peterson 2011; Jiménez-Valverde *et al.* 2011). By using distributional data from both native and other invaded ranges, possibly small niche shifts could be incorporated into ecological niche models.

To compare the invasion risk maps produced with both calibration scenarios, we fitted ecological niche models using data from the native and the pooled range for the wild boar. Our niche models were therefore calibrated with: 1) occurrences from the wild boar's native distribution (native-based models); or 2) occurrences from all distribution information available (pooled-range-based models) (see Fig. S1). All models were projected worldwide. We randomly partitioned wild boar occurrence data into two subsets of calibration (75% of data), and validation (remaining 25%). That data-splitting process was repeated 100 times, in a cross-validation procedure, maintaining the species observed prevalence unchanged. Those occurrences, coupled with the five previously chosen environmental predictors, were used to model the wild boar potential distribution.

Diverse techniques have been proposed for estimating species climate niches and potential distributions (Franklin 2009). These methods usually aim to provide a mathematical link between occurrence information for the species and the environmental predictors associated to the location of those occurrences. In this work, ecological niche models are solely meant to provide estimates of the wild boar distributional potential. Niche comparisons were

297 performed using the methods described in the previous section, following Broennimann
298 (2012). We therefore chose methods best suited to estimate the potential distribution of a
299 species, or invasion risk maps (Jiménez-Valverde *et al.* 2011). In this work, chosen methods
300 do not strongly rely on true absence information and usually lead to overprediction, an
301 intrinsic artifact to the very nature of invasive species (Jiménez-Valverde *et al.* 2011).

302

303 Three different presence-only and presence-pseudoabsence modeling techniques were used:
304 Bioclim, Mahalanobis distance and Support Vector Machine. In Bioclim, environmental
305 predictors of species occurrences are treated as multiple distributions of uni-tailed
306 percentiles. The values of each cell grid are evaluated to determine their position in the
307 distribution percentiles. Bioclim then compares the predictor values in a grid cell to the
308 distribution percentiles of the known occurrences of the species to calculate the relative
309 suitability of a given grid cell (Graham & Hijmans 2006; Hijmans *et al.* 2013). Therefore,
310 values of predictor variables closer to the $50^{th}$ percentile (the median) are considered the most
311 suitable for species. Distribution tails are not distinguished, that is, the $10^{th}$ percentile is
312 equivalent to the $90^{th}$ percentile.

313

314 Species distribution models based on Mahalanobis distance consider the correlations of
315 environmental variables, are scale-independent and useful to determine the similarity
316 between a known sample and an unknown sample (Hijmans *et al.* 2013). Calculations in the
317 mahal algorithm are based on the Mahalanobis distance (Mahalanobis 1936). The highest
318 possible value is a function of the correlation between variables in the data set. Consequently,

similarity values are not dependent on the scale of measurements. Bioclim and Mahalanobis distance are presence-only methods (Franklin 2009). Bioclim models were fitted with the *bioclim* function, and Mahalanobis distance models with the *mahal* function, from the R package *dismo* (Hijmans *et al.* 2013).

Support Vector Machine models are a machine-learning technique to analyze data and recognize patterns (e.g. species presences) (Karatzoglou, Smola & Hornik 2016). Support Vector Machine are useful for classification and regression analysis, and usually exhibits good performance under several conditions (Karatzoglou *et al.* 2016). Support Vector Machine is a presence-background method (Franklin 2009), for which models were fitted using the function *ksvm* from R package *kernlab* (Karatzoglou *et al.* 2016). We used an epsilon regression (*eps-svr*) with binary numeric response. All non-binary variables were scaled to mean zero plus variance. The argument *kpar* contains the parameters to be passed on to the kernel function and calculates the appropriate sigma value for the regression. The *ksvm* function, i.e. the kernel function, was used in both training and prediction. Model fitting is performed on output data, via a 3-fold cross-validation on the training dataset, which is the suggested procedure (Karatzoglou *et al.* 2016).

Continuous predictions of habitat suitability derived from the three previously described ecological niche models were converted to binary projections. For that, we found the threshold with maximum sensitivity and specificity values in the relative operating characteristic (ROC curve). Then, we calculated the True Skills Statistics (TSS), a measure

of model performance that corrects for the dependence on the prevalence of the modelled. The TSS is the measure of choice for presence-absence predictions and ranges from -1 to +1 (Allouche, Tsoar & Kadmon 2006). Values close to +1 indicate good prediction and values equal or smaller than zero are not better than random predictions (Allouche *et al.* 2006).

Ensembles of forecasts tend to produce more robust predictions and reduce variability related to modeling methods used (Diniz-Filho *et al.* 2009). We therefore created an ensemble of gridded potential distribution maps, originated from the three methods we used here. Ensembles were then created by weighting each model projection (habitat suitability map) according to model performance to discriminate them in terms of accuracy, and only models with TSS > 0.5 were used in final models of potential distribution.

## Results

Patterns of niche shift during wild boar invasion were not similar across all studied regions (Table 1). Niche overlap (in terms of Schoener's *D*) between native and invaded niches was overall low (Table 1). The wild boar populations from Australasian region presented the highest values of niche overlap with the native populations of the species (Schoener's $D = 0.4 \pm 0.03$), compared to the Neotropical (Schoener's $D = 0.3 \pm 0.06$) and the Nearctic (Schoener's $D = 0.2 \pm 0.02$). However, we found no evidence that the invaded populations' niches from any of the analyzed regions are identical to their native counterparts, although in the Nearctic they were more similar than expected by chance (Figs. S2, S3 and S4).

363 The hypothesis that native and exotic niches are indistinguishable (i.e. niche equivalence)
364 was rejected for all biogeographical regions. However, the hypothesis that niche overlap falls
365 within the 95% confidence limits of the null distributions (i.e. niche similarity) was rejected
366 only for the Neotropical and Australasian region. In these regions, the wild boar's realized
367 niche was apparently different from the one belonging to native populations.

368

369 Although some apparent niche shifts were observed, niche stability was high overall
370 ($Stability_{mean}$ = 0.99 ± 0.006) and niche expansion was low ($Expansion_{mean}$ = 0.01 ± 0.006)
371 in all regions. Niche shifts indicated by rejection of null hypotheses of niche similarity were
372 explained by the process of niche unfilling ($Unfilling_{mean}$ = 0.12 ± 0.14). The proportion of
373 climate conditions present in the native range, but unoccupied by exotic populations ranged
374 from 1% in the Nearctic, to 8% in Australasia and up to 28% in the Neotropics.

375

376 Because we found evidence for niche conservatism, we created invasion risk maps based on
377 climate suitability, using ecological niche models. Native-based models had a slightly poorer
378 accuracy than pooled-range-based models ($TSS_{mean}$=0.62±0.1 and $TSS_{mean}$=0.68±0.06,
379 respectively). Native-based models also accurately predicted most areas where wild boar is
380 known to have invaded in all but the Australasian region (Fig. 2). The Afrotropical
381 biogeographical region was not used for niche comparison in this work due to the small
382 number of valid occurrences (n = 2). Although we did not calibrate models with occurrences
383 for that region, both ecological niche model calibration scenarios used here (native *vs* pooled

384 range) indicated high climatic suitability for the wild boar on central and southeastern Africa
385 (Fig. 2).

386

## 387 Discussion

388 We found that during the wild boar invasion into the Neotropical, Nearctic and Australian
389 regions, niche stability was high and niche expansion was low. Although native and exotic
390 populations' niches were not equivalent (*sensu* Peterson et al., 1999), climatic matches
391 among occupied ranges were greater than expected by chance (*sensu* Graham et al., 2004) in
392 only one out of three regions analyzed. Niche stability was however corroborated by niche
393 overlap measures (*sensu* Broennimann et al., 2012) and also by congruent broad-scale
394 predictions of ecological niche models calibrated with native and pooled range data (*sensu*
395 Peterson, 2003). Niche conservatisms is arguably one of the main processes that allows for a
396 species to invade different areas across the globe (Peterson 2011; Strubbe *et al.* 2015; Pyron
397 *et al.* 2015). Although phylogenetic changes in species fundamental niches are expected
398 during the speciation processes (Pyron *et al.* 2015), such changes are rarely observed at the
399 timescale of man-made introductions (Peterson 2011).

400

401 Even though niche conservatism seems to be an *a priori* assumption for predicting potentially
402 invadable areas (Jiménez-Valverde *et al.* 2011), observation of niche changes are
403 increasingly reported (Broennimann *et al.* 2007; Tingley *et al.* 2014; Early & Sax 2014). The
404 validity of those changes is however questioned due to the recent unraveling of processes
405 driving niche shifts (Guisan *et al.* 2014). If species, in their invaded range, only occupy a

406 subset of the environmental conditions that they are usually found in their native range,
407 classic statistical tests may indeed find differences among realized climatic niches. Those
408 differences nevertheless do not arise from expansion into non-analogous climate, as expected
409 from evolutionary adaptation. Niche unfilling might indeed be the pure result of ongoing
410 colonization and slow dispersal (Petitpierre *et al.* 2012; Guisan *et al.* 2014; Strubbe *et al.*
411 2015). A single snapshot in time may therefore not be sufficient to capture nuances of these
412 processes. Observed changes on realized niches may in fact mislead understanding of niche
413 shifts during biological invasions. Here, comparisons of native *vs* exotic populations revealed
414 that niches were more similar than expected by chance in the Nearctic, although not
415 equivalent in any analyzed region, and that differences may be explained by niche unfilling,
416 rather than niche expansion (Guisan *et al.* 2014). Observed niche shifts due to unfilling of
417 environmental space have already been reported for several non-native vertebrate species,
418 including the wild boar (Strubbe *et al.* 2013, 2015).

419

420 Colonization history and propagule pressure also affect observed niche changes during
421 biological invasions. Niche unfilling seems to be larger for species introduced recently and
422 into a small number of locations, compared to those with ancient colonization history and
423 introduced in several points in space (Strubbe *et al.* 2015). In this work, niche unfilling was
424 substantially higher for the Neotropics, compared to other locations. Wild boar importation
425 into the Neotropics has a 200 year long history (Skewes & Jaksic 2015). However, recent
426 waves of introduction on the 1990s for pig-farming and game hunting, followed by escape
427 and inter-country dispersal (Skewes & Jaksic 2015; Pedrosa *et al.* 2015) have led to explosive
428 population growth in the Neotropics (Pedrosa *et al.* 2015). Because we found 28% of niche

unfilling for the Neotropical region, our results indicate that the invasive potential of wild boar might be larger than expected so far. Preventing the expansion of wild boar distribution into Neotropical species-rich areas such as the Amazon, coupled with potential economic loss, thus requires specific management towards population control in areas already invaded.

Because the niche of non-native populations of wild boars is a subset of its native counterparts' niche, ecological niche models should lead to accurate predictions of potentially invadable areas (Strubbe *et al.* 2015). We found that models calibrated with occurrences within the native distribution indeed predicted areas reportedly struggling with wild boar population expansion, such as the south and southeastern Brazil (Pedrosa *et al.* 2015), eastern USA (Pimentel *et al.* 2005) and eastern Australia (Spencer & Hampton 2005). In other words, models calibrated with native and pooled ranges led to convergent predictions, thus suggesting that newly occupied areas are climatically similar to the ones the wild boar was already adapted to. Those convergences imply that evolutionary markers from climatic constraints across the native range are still evident on populations inhabiting exotic ranges (Pyron *et al.* 2015).

We found a remarkable convergence on potentially invadable areas for the Afrotropical region. Although no data from that region was used to calibrate ecological niche models, both calibration scenarios predicted high climatic suitability for the wild boar in central and southeastern Africa. The Suidae family is a monophyletic group of Cetartiodactyla, composed of 17 species and originated in Africa (Frantz *et al.* 2016). That origin of extant

451 species is relatively recent – less than 5.3 Ma – and many lineages have and continue to
452 hybridize (Frantz *et al.* 2016). Climatic constraints on species realized niche may be the result
453 of adaptation to climates in which species have evolved (Pyron *et al.* 2015). If fundamental
454 niches are phylogenetically conserved and climate-related evolutionary markers are indeed
455 preserved on related lineages (Pyron *et al.* 2015), then the high climatic suitability exhibited
456 for the wild boar may in fact be shared with other Afrotropical Suidae species. Furthermore,
457 the diversity of Suidae species in Africa probably prevented wild boar invasion, because
458 humans bred other suids (such as the bushpig *Potamochoerus larvatus*) and transported them
459 through the mainland and towards Mayotte, Comoros, Madagascar and other islands (Frantz
460 *et al.* 2016). Testing whether phylogenetic niches are preserved among members of the
461 Suidae family is yet to be attempted, but could shed substantial light to the processes driving
462 speciation in that taxa.

463

464 One exception to the ecological niche models' predictive ability was nevertheless found.
465 Models calibrated with native occurrences were less able to predict wild boar's exotic
466 occurrences in Australasia, compared to the other regions. Domestic pigs were first stablished
467 in Australia in 1788 and recreational hunting has been common practice among Caucasian
468 and Aboriginal groups since then (Bengsen *et al.* 2014; Meurk 2015). Pig hunting is therefore
469 part of subsistence and social practices and contributes substantially to regional economies
470 (Meurk 2015), despite long-lasting attempts to eradicate feral pig populations in Australian
471 territory (Bengsen *et al.* 2014). Illegal transportation for game hunt and escapes from pig
472 farms probably increase propagule pressure all over Australia, thus leading to species
473 temporary occupancy of sub-optimal climates. Those populations occupying marginal

474 climates are characterized by sink dynamics and are not expected to persist in time (Colwell
475 & Rangel 2009; Soberón & Nakamura 2009).

476

477 Also, some of the records from central Australia are from pigs following flooding rivers
478 downstream into Lake Eyre. This is not driven by local climatic events, but rainfall far away
479 in the upstream reaches of the catchments, and so correlations between climate and
480 occurrence is less likely here. Because native-based models were less able to predict wild
481 boar occurrence in the Australasian region, we suggest that predictive maps of invasion risk
482 for that region should be calibrated with pooled range calibration scenarios. Although overall
483 broad-scale differences were small, including all known occurrences of an invasive species
484 allows incorporation of possible non-equilibrium source-sink dynamics and their outcomes,
485 which improves invasion risk assessments at regional scale (Peterson 2011; Jiménez-
486 Valverde *et al.* 2011).

487

488 Wild boars, like other Suidae members, have a limited ability to eliminate heat. They lack
489 functional sweat glands, have a thick hairy skin and tend to accumulate subcutaneous fat
490 (Manner & McCrea 1963; Fernández-Llario 2005; Bracke 2011). We expected that wild
491 boars would thus preferentially occupy low temperature sites, such as high altitudes and high
492 latitudes, to prevent hyperthermia. However, all models predicted high climatic suitability in
493 warm areas, such as tropical America and Africa. Also, the wild boars' native distribution
494 includes the low-latitude Indian horn, southern China and The Philippines. The occupancy
495 of warm climates suggests that mechanisms other than physiology have evolved in wild boars

to prevent overheating. In response to increased temperature, pigs usually exhibit a series of behavioral patterns, of which the most obvious is wallowing (Olczak, Nowicki & Klocek 2015). Wallowing helps wild boars eliminate heat and may have a sexual function in males (Fernández-Llario 2005). We believe that behavioral flexibility may further allow the wild boars to occupy a wide range of climate conditions and thus overcome many physiological limitations, while also enhancing its invasive potential.

The wild boar is considered one of the worst invasive alien species in the world (Lowe *et al.* 2000). Its rapid and large-scale spread into many places worldwide is an issue of great concern for areas as diverse as agriculture, economy and biodiversity conservation. We found that, while niche conservatism explains invasion patterns, the broad native distribution of wild boar is suggestive of a pre-adaptation to a wide array of climate conditions. That large climatic tolerance is probably related to the species successful invasive potential, which can have unprecedented proportions on newly colonized regions, such as the Neotropics. Our results explain the observed invasive success of the species on several parts of the world, and highlight potentially invadable areas to the wild boar.

## Authors' contributions

LPS, BRR, MWH, AP, MP and RL conceived the ideas and designed the methods; LPS and MWH collected the data; LPS and BRR analysed the data; LPS led the writing; BRR, MWH, AP, MP and RL assisted writing and reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Data Accessibility

Climate data used in this work can be downloaded at www.worldclim.org/version1. Wild boar occurrences were collected on freely available web sources, listed in M&M section. Additional data was obtained from a literature survey, which is provided as supplementary material, alongside with the spreadsheet containing all occurrences collected in this work. All R codes used in this paper are based open-source packages, available at The Comprehensive R Archive Network (cran.r-project.org). All R scripts used in niche overlap and ENM assessments can be downloaded at

http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Full occurrence dataset, plus their biogeographical origin, used in the modeling procedures of this work

**Table S1.** Supplementary literature.

**Table S2.** Summary of loadings from factorial analysis.

**Fig. S1.** Distribution of wild boar occurrences and calibration scenarios.

**Fig. S2.** Summary of niche equivalence and similarity tests for comparisons between native and Neotropical populations.

**Fig. S3.** Idem Fig. S2, for comparisons between wild boar populations from native and Australasian region.

**Fig. S4.** Idem Figs. S1 and S2, for comparisons between wild boar populations from native and Nearctic region.

**Fig. S5.** Niche shifts observed during wild boar invasion into the Neotropical, Australasian and Nearctic biogeographical regions.

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## *Figure legends*

**Fig. 1.** Distribution of wild boar *Sus scrofa* around the world. Violet polygon indicates the species native distribution, according to the IUCN. Dark pigs indicate wild boar occurrences considered native in this study, and pale pigs represent occurrences considered exotic. Only some occurrences used in this work are shown.

**Fig. 2.** Climate suitability and potentially invadable areas for the wild boar *Sus scrofa*. On the left, predictions are based on models calibrated solely with occurrences within the species native range (native-based models). On the right, models were calibrated with all locations where the wild boar is known to occur (pooled-range-based models). Continuous predictions are shown on top, where reddish colors indicate high suitability and bluish colors, low suitability. Binary predictions are presented on the downside of the picture, where red color indicates predicted presence and white color, absence.